WETLANDS, Vol. 27, No. 2, June 2007, pp. 211–223

SOIL SEED BANK ANALYSIS OF PLANTED AND NATURALLY REVEGETATING THERMALLY-DISTURBED RIPARIAN WETLAND FORESTS

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Abstract: Accelerating the reestablishment of a mature, biotic community following a disturbance is a common goal of restoration ecology. In this study, we describe the relative successional status of a recently disturbed riparian seed bank when compared with less recently disturbed and undisturbed systems, and the short-term effects of restoration on seed bank development within the recently disturbed system. The study location, the U.S. Department of Energy's Savannah River Site in South Carolina, provides a unique opportunity to investigate the development of wetland seed banks following a severe disturbance, in this case the release of elevated temperature and flow effluent from nuclear reactor operations. To assess the recovery of wetland seed banks over time, we compared seed banks of naturally recovering riparian corridor and swamp delta sites of two different ages since disturbance (nine years and 30 years) with undisturbed forested corridor and swamp sites. To assess the potential effects of restoration efforts (site preparation and planting of seedlings) on seed bank development, we compared seed banks of naturally recovering (unplanted) and planted riparian corridor and swamp delta sites in the more recently disturbed system. We expected total germinants and species richness to be highest in the recently disturbed sites and decline as wetland systems matured. Within recently disturbed sites, we expected planted sites to have higher abundance and richness than unplanted sites. We also expected a greater abundance of woody species in the undisturbed forested sites. The number of germinants differed among the sites, ranging from 748 individuals per m^2 in the undisturbed swamp area to 10,322 individuals per m^2 in the recently disturbed planted swamp delta. When corridor and delta sites within a stream system were combined, the mean number of germinants was greater in the recently disturbed system, intermediate in the 30-year (mid-successional) system, and lowest in the undisturbed system. Seed banks from the recently disturbed and mid-successional sites were more similar in composition than they were to the undisturbed systems. Across all stream systems, riparian corridors had greater mean species richness than swamp deltas, though differences in seed bank abundances were not significant. Sedges and rushes were the predominant life forms in the recently disturbed and mid-successional sites, while undisturbed sites had a greater proportion of herbs and woody seedlings. In addition, there were more germinants from planted sites than from unplanted sites. The dominance by early successional species at recently disturbed planted sites may be an unintended consequence of site preparation treatments, and such potential effects should be recognized and weighed during the development of restoration plans.

Key Words: riparian restoration, successional gradient, thermal disturbance

INTRODUCTION

Historically, riparian systems have been targets for human exploitation (Petts 1984, Delcourt et al. 1993, Delong 2005, Smock et al. 2005, Sternberg 2006), and often impacts from disturbances are long-lasting. In forested floodplain corridors, disturbances to the hydrologic regime may not only affect the area at the origin of impact, but may also exert some level of disturbance along downstream regions. Following a "severe disturbance" (i.e., one in which both the extant vegetation and seed bank are destroyed), reestablishment of a mature riparian plant community may be slow as propagule dispersal becomes more dependent on hydrochory (Dulohery et al. 2000). Further impeding revegetation, adjacent upland forests typically are composed of tree species not adapted to wet conditions, and seeds of characteristic riparian species may be locally scarce. As such, severely disturbed upstream regions may become effectively isolated from less impacted downstream areas, where surviving vegetation remains and propagules are available for dispersal. In such situations, it may be desirable to plant woody species characteristic of later successional riparian communities to enhance establishment and seed availability of selected species, stabilize substrates, dampen abiotic environmental fluctuations, and ultimately, accelerate the successional return of a mature wetland community.

Under natural conditions, secondary succession may be viewed as a gradual transition from ruderal vegetation, in which resources are allocated to the rapid production of seeds (Barbour et al. 1987), to competitive species that maximize vegetative growth or to stress-tolerant vegetation (Grime 1977). Consequently, along a successional gradient, the importance of a persistent seed bank may decrease. Such a trend of decreasing density and diversity of propagules in the seed bank has been well documented in old-field and temperate deciduous forest succession (Symonides 1986, Pickett and McDonell 1989, Roberts and Vankat 1991). Similarly, in a synthesis of herbaceous and forested seed bank studies, Thompson (1978) reported that the density of buried seeds decreased with increasing successional age. Decreasing importance of seed banks over time has been attributed to decreases in the numbers of seeds produced by later successional species and seed longevity, as well as to the increase in seed predation as mature forests develop (Milberg 1995). Similarly, one might expect that seed bank abundance and richness will decline as disturbed riparian systems recover and presumably approach a vegetation structure similar to mature undisturbed sites.

Annual plant species, prevailing in initial stages of succession and becoming less dominant later, usually produce large numbers of persistent seeds (Fenner 1987, Huston and Smith 1987, Prach et al. 1997). In some terrestrial and river floodplain forest studies, herbaceous species dominated seed banks, while woody species were virtually absent (Oosting and Humphreys 1940, Livingston and Alessio 1968, Donelan and Thompson 1980, Pickett and McDonnell 1989, Matlack and Good 1990, Middleton 2003). Schneider and Sharitz (1986) and Titus (1991), however, reported a modest woody component in seed banks of mature southeastern riverine swamp forests. Based on these observations, one might expect riparian seed banks to be dominated by herbaceous species but with woody species increasing in abundance and richness along a successional gradient.

We assessed riparian wetland seed bank abundance and species richness along successional and hydrologic gradients at the U.S. Department of Energy's Savannah River Site (SRS) near Aiken, S.C. Previous industrial protocol at the SRS entailed pumping water from the Savannah River for the cooling of nuclear production reactors. These thermal effluents were discharged directly from the reactors into the headwaters of several SRS streams that are tributaries of the Savannah River. The high temperatures (40–70°C) and elevated flows (one to two orders of magnitude above normal conditions) destroyed virtually all vegetation and propagules in the riparian corridors (Nelson et al. 2000), and eroded sediment was transported downstream to create delta areas where the streams entered the river floodplain (Sharitz et al. 1974a). When reactor operations ceased, streams were allowed to revegetate naturally, or restoration was initiated. Restoration focused on the most recently disturbed riparian system, Pen Branch, and entailed site preparation and planting of selected woody seedlings characteristic of later-successional riparian communities (Nelson et al. 2000).

The efficacy of restoration efforts, especially in the short term, may be difficult to assess by investigation of the extant community alone. We propose that in the early years following restoration, a seed bank level investigation may reveal potential trajectories of future vegetative communities. Due to the effect of site preparation treatments, we anticipated that seed banks of planted areas would have a greater abundance of propagules and number of species than seed banks of unplanted areas. We did not, however, expect the planting to enhance the woody component of the seed banks at this time, since few if any of the seedlings had reached reproductive status (Landman 2000).

In summary, we compared the seed abundance (number of germinants) and species composition in seed banks of planted and unplanted riparian corridor and swamp delta sections in the most recently disturbed system, Pen Branch. We also compared the seed banks of Pen Branch sites with those of a similar stream, Steel Creek, that had been naturally recovering for 30 years (mid-successional) and those of undisturbed riparian and swamp systems (Meyers Branch and the Savannah River swamp). We hypothesized that 1) seed bank abundance and species richness would be greatest in Pen Branch, intermediate in Steel Creek, and lowest in Meyers Branch and the Savannah River swamp, 2) herbaceous species would be dominant, but seeds of woody species would have higher relative abundance in the undisturbed sites than in the disturbed sites,

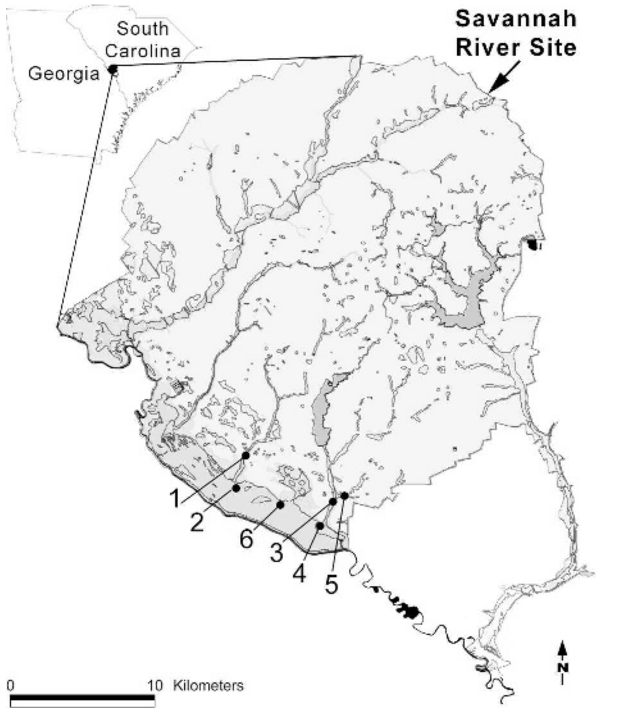

Figure 1. Location of the Savannah River Site in S.C., USA (inset) and the location of study sites on the Savannah River Site. 1 = Pen Branch corridor (two sites: planted and unplanted), 2 = Pen Branch delta (two sites: planted and unplanted), 3 = Steel Creek corridor, 4 = Steel Creek delta, 5 = Meyers Branch corridor, 6 = Savannah River swamp. Darker areas on the Savannah River Site map indicate wetlands and surface waters.

and 3) within Pen Branch, seed banks of planted sites would have greater abundance of propagules and species richness than those of unplanted sites.

MATERIALS AND METHODS

Study Area

Riparian corridor and delta regions of three third-order blackwater streams on the SRS were the focus of this study (Figure 1). The climate of this region of the Upper Coastal Plain is temperate with a mean monthly temperature of 10°C in the winter and 30°C in the summer (Dukes 1984), and mean annual precipitation is approximately 120 cm. The floodplain soils have poor drainage and are generally classified as Fluvaquentic Inceptisols, with high spatial variability in texture and organic-matter content (Dulohery et al., 2000). Dominant canopy trees of the floodplains of undisturbed streams of the area include *Liquidambar styraciflua*, *Quercus laurifolia*, *Quercus nigra*, *Acer rubrum*, and *Fraxinus pennsylvanica* (Workman and McLeod 1990). Undisturbed forests of the Savannah River floodplain contain these species along with *Quercus lyrata* and *Celtis laevigata* in higher elevation sites and swamp forests of *Taxodium distichum* and *Nyssa aquatica* in poorly drained areas (Workman and McLeod 1990).

The three stream systems are assumed to have been floristically similar before operation of the SRS nuclear reactors. Pre-disturbance (1951) aerial photography shows mostly uniform, closed canopy bottomland hardwood forests along the stream floodplains, interspersed with *Taxodium distichum-Nyssa aquatica* swamp forests where they flow into the floodplain of the Savannah River swamp (Sharitz et al. 1974b). Reactor operations and release of thermal effluents began on similar dates in both disturbed streams (Pen Branch and Steel Creek; Table 1), and the intensity of the disturbance regime in both impacted streams was comparable.

Pen Branch received thermal discharges for 35 years (Table 1). The high temperature resulted in complete mortality of the original vegetation in large areas of the floodplain (Nelson et al. 2000), and the elevated flow caused scouring of the channel and widespread erosion (Kolka et al. 2000). Consequently, massive amounts of sediment were transported and deposited downstream, creating an alluvial fan-shaped delta where Pen Branch meets the Savannah River floodplain. When reactor discharges ceased in 1989, 88 ha of bottomland hardwood forest in the corridor and 148 ha of swamp forest in the delta area had been destroyed (Dulohery et al. 1995). By 1990, early successional woody species had colonized the corridor floodplain (Table 1), but there was virtually no regeneration of canopy tree species because the prolonged exposure to thermal discharges had eliminated seed sources and living root stocks (Nelson et al. 2000). In the delta area, dense cover of herbaceous wetland plants, especially *Typha latifolia* and *Scirpus cyperinus* (Table 1), likely prevented reestablishment of *Taxodium distichum* and *Nyssa aquatica* even though seeds might have been transported by water into the area (Nelson et al. 2000).

Riparian forest restoration began in Pen Branch in 1993 and entailed site preparations and planting of native woody seedlings. Corridor areas to be planted were treated with herbicide (glyphosate) and burned, while areas to be planted in the delta were herbicide treated only; these treatments were intended to reduce competition from naturally established early successional plants and increase resource availability. Species assemblages selected for reintroduction mimicked pre-disturbance forest composition. Seedlings of *Quercus nigra*, *Q. pagoda*, *Q. shumardii*, *Q michauxii*, *Carya glabra*, *C. aquatica*, *Nyssa biflora*, *N. aquatica*, *Diospyros virginica*,

Table 1. Disturbance history and dominant vegetation cover of the Pen Branch, Steel Creek, and Meyers Branch riparian corridor sites; the Pen Branch and Steel Creek delta sites; and the Savannah River swamp site, on the Savannah Rivers Site near Aiken, S.C., USA.

Wetland Site	Period of Thermal Disturbance	Dominant Vegetation at Time of Study	
		Riparian Corridor	Swamp/Delta
Pen Branch[1]	1954–1989	*Salix nigra*, *Alnus serrulata*, *Morella cerifera*, *Cephalanthus occidentalis*, *Rhus copallinum*; early successional wetland and upland herbs	*Salix nigra*., *Typha latifolia*, *Scirpus cyperinus*
Steel Creek[2,3]	1953–1968	*Acer rubrum*, *Salix nigra*, *Morella cerifera*; perennial wetland herbs and graminoids	*Cephalanthus occidentalis*, *Acer rubrum*, *Salix* spp., *Fraxinus* spp.; perennial wetland herbs and graminoids
Meyers Branch[2]	none	*Acer rubrum*, *Taxodium distichum*; sparse perennial wetland herbs	______
Savannah River Swamp[4]	none	______	*Taxodium distichum*, *Nyssa aquatica*, *Fraxinus caroliniana*; sparse perennial wetland herbs

Data from previous studies: [1]Nelson et al. 2000, [2]McArthur et al. 1986, [3]Dunn and Sharitz 1987, [4]Sharitz et al. 1990.

Fraxinus pennsylvanica, *Platanus occidentalis*, and *Taxodium distichum* were planted in strips in the corridor site, and *F. pennsylvanica*, *N. aquatica*, and *T. distichum* were planted in the delta area (Nelson et al. 2000). In both corridor and delta regions, unplanted areas were located in strips between planted areas so that the effect of site preparation and planting could be compared to the natural vegetation recovery.

Steel Creek received reactor cooling waters from 1953–68 (Table 1). As in Pen Branch, thermal discharge destroyed the vegetation along the stream channel and adjacent floodplain and transported large amounts of sediment to create a delta where the creek enters the river floodplain. Twenty years after reactor operations ceased, the vegetation was dominated by early and mid-successional trees and shrubs, especially *Salix* spp. (Table 1). There was virtually no regeneration of *Taxodium distichum* or *Nyssa aquatica* in the delta region (Dunn and Sharitz 1987). No planting was conducted within the Steel Creek corridor or delta.

Meyers Branch flows into the upper corridor of Steel Creek (Figure 1). This riparian community has been free from anthropogenic disturbance except for selective logging in the early 1950s and is presumed to be vegetatively similar to pre-disturbance Pen Branch and Steel Creek (McArthur et al. 1986). A *Taxodium distichum-Nyssa aquatica* swamp forest on the Savannah River floodplain served as an undisturbed comparison for the stream delta regions (Figure 1, Table 1).

The three stream systems, all located within 6 km of each other (Figure 1), represent a successional gradient from a recently disturbed system (Pen Branch), to a mid-successional system undergoing natural recovery for 30 years (Steel Creek), to a relatively undisturbed reference system (Meyers Branch corridor and the Savannah River swamp). To minimize differences between sites, the riparian corridor areas were similar in soil composition, located at similar elevations, and similar in stream order. Delta regions also were similar in soil composition and located at similar elevations (Figure 1). Despite measures to limit between-site variation, we acknowledge that these chronosequences are inherently pseudo-replicated. The selected stream systems are not true "replicates," and both impacted streams were recovering from disturbance at different times when environmental conditions and availability of dispersing propagules may have varied. Despite these limitations, these riparian systems provide a framework to compare seed banks across a successional gradient and assess any effect of planting on early seed bank development.

Sampling Design

Riparian corridor samples were collected from two sites on Pen Branch (one planted and one unplanted area), one site on Steel Creek, and one site on Meyers Branch (Figure 1). At each site, five transects parallel to the direction of flow were placed at equal distances from each other across the width of the corridor. Distances between transects differed among the sites, depending upon the width of the stream corridor. In Pen Branch, transect lengths encompassed the entire length of the planted or unplanted strip (140–240 m). In Steel Creek and Meyers Branch, transects were 240 m unless constrained by natural boundaries. The streams at all of these sites are very narrow, shallow and braided; thus, some transects crossed small channels.

Delta samples were collected from two sites on Pen Branch (one planted and one unplanted area), one site on Steel Creek, and one site in the Savannah River swamp (Figure 1). At each delta or swamp site, five transects, the first positioned parallel to the upland edge, were placed parallel and equidistant from each other out into the delta. In Pen Branch, transect lengths encompassed the entire planted or unplanted strip (80–100 m); Steel Creek and the Savannah River swamp transects were 100 m unless limited by natural boundaries. Transects in both corridor and delta sites were divided into 10 sampling points equally spaced along the upstream-downstream gradient. If a sample point occurred in an open channel, it was moved the minimum distance along the transect to place it on the floodplain.

Seed Bank Sampling

Seed bank samples were collected during June and July of 1998. At each of the 10 sample points along each transect, five soil cores were collected from the four corners and center of a 1-m^2 plot. Soil cores were taken with a standard "cup-cutter" (Livingston and Allessio 1968) that extracted samples 10 cm in diameter and 10 cm deep. This lower limit was considered adequate because decline in seed banks is often exponential (Leck 1989), with relatively small numbers of seeds below 10 cm (Leck and Simpson 1987). All five samples from each plot were pooled and labeled in the field. They were then transported to the University of Georgia's Savannah River Ecology Laboratory (SREL) where they were held under cool moist conditions for no more than two weeks.

Samples from each transect were pooled again and thoroughly mixed to form two macro-samples, each consisting of five plot samples (half the length of the original transect). Aggregation of small samples distributed within an area may be effective in capturing seeds of species with patchy seed bank distributions while maintaining a reasonable number of samples for germination tests, and it has been performed in other wetland seed bank studies (e.g., Mulhouse et al. 2005, Capon and Brock 2006, De Steven et al. 2006). This pooling of samples resulted in 10 macro-samples per site (two per transect). A 2-liter sample of soil was taken from each macro-sample, and large roots, rhizomes, and litter were removed by hand. These samples were placed in 52 $\times$ 26 $\times$ 6 cm flats containing 2.5 liters of vermiculite potting soil. The flats were placed randomly inside large plastic-lined frames in a greenhouse. Water added to the frames was absorbed through holes in the bottoms of the flats to maintain soil moisture similar to field conditions. Control flats, containing only vermiculite potting soil, were placed at five locations inside the greenhouse to detect invading species. Temperature was maintained close to outdoor ambient conditions. Locations of flats in the greenhouse were reorganized three times during the experiment to minimize micro-climatic differences.

Seedling emergence was used to determine seed bank composition (Poiani and Johnson 1989, Gross 1990, Kirkman and Sharitz 1994, Mulhouse et al. 2005). Newly germinated seedlings were identified to the most precise taxonomic level possible, usually species, and removed from flats to prevent crowding. Unidentified seedlings were transplanted to empty flats where they were grown, allowed to flower, and identified at the University of Georgia herbarium (nomenclature follows USDA NRCS 2006). Plants that could not be identified to species were recorded by genus or family, or reported as unknown. Soils in the flats were stirred after six months to encourage further germination. Seed bank emergence was monitored for seven months, until germination noticeably declined. Because the samples were collected in early summer, we assumed that seeds dispersed the previous growing season had been naturally stratified. Our methods may have underestimated species with seeds that germinate in early spring, or species for which seed stratification or germination requirements were not met. Homogenization of samples also resulted in all seeds, regardless of their depth in the soil, being exposed to shallow soil conditions for germination.

Statistical Analysis

Plant species were distinguished into five major life forms: herbs, sedges and rushes, grasses, trees and shrubs, and vines (Appendix 1). The percentage of life forms at each site was calculated by dividing the number of germinants of each life form by the total number of germinants from the site. Unidentified plants were included in site abundance calculations, but they were not used in calculating site species richness or in dissimilarity indices. Unknowns comprised a very small percent of the seed bank (0.36%).

Seed bank differences in species richness and abundance between sites were evaluated using an ANOVA model (PROC GLM, 7.0 for Windows; SAS 1998). Within-site and between-site dissimilarities were calculated using Bray Curtis, square root of Bray Curtis, and Jaccard ANOSIM indices (Digby and Kempton 1987). In addition to demonstrating that seed banks of the sites are significantly distinct, this analysis allowed for statements to be made concerning the relative similarity of one seed bank site (or group of seed bank sites) to another. Similarity coefficients can range from zero (complete dissimilarity) to one (total similarity). In all site dissimilarity analyses, sampling points from transects located near the edges of the floodplain corridors (transects 1 and 5) and mid-corridor transects (transects 2, 3, and 4) were analyzed separately to minimize compositional differences based solely on the position of sampling points across the riparian corridor. In the three delta regions, only the first transect was near the edge and was analyzed separately. Resulting dissimilarities between sites were tested for significance by the Kruskall-Wallis test (Anderson et al. 1994). The Bray Curtis index is the primary dissimilarity index reported in this study. Other dissimilarity analyses are reported only if they contradicted results observed from the Bray Curtis index.

RESULTS

Seed Bank Species Richness

Among all sites, the seed banks contained 61 species, of which 56 were herbaceous and five were woody. The total number of species per site ranged from 25 in the Steel Creek delta to 44 in the unplanted corridor of Pen Branch (Appendix 1), and the mean species richness differed across sites ($F_{7,67} = 24.68$, $P = 0.0001$; Figure 2). Of the woody species, four germinated from the undisturbed forest floodplain at the Meyers Branch corridor and three from the undisturbed Savannah River swamp; these included *Liriodendron tulipifera*, *Nyssa aquatica*, and *Taxodium distichum*. The two woody species found in the seed banks of the Pen Branch planted sites were *Liriodendron tulipifera* and the shrub *Rhus coppalinum*. The Pen Branch unplanted corridor and the Steel Creek delta seed banks had no woody species.

When corridor and delta sites were grouped by stream, the mean seed bank species richness was highest in Pen Branch; however, neither the planted or unplanted Pen Branch sites differed from those of the Steel Creek system (Figure 2). In addition, both Pen Branch and Steel Creek had greater seed bank

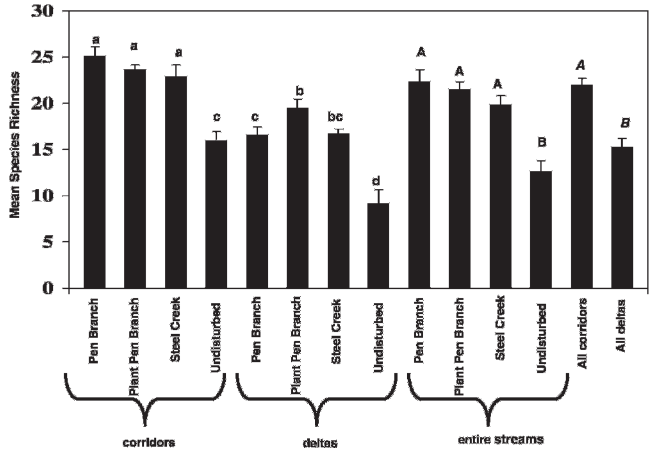

Figure 2. Mean species richness of the seed bank of the Pen Branch, Steel Creek, and the undisturbed Meyers Branch riparian corridor sites; Pen Branch and Steel Creek delta sites; the undisturbed Savannah River swamp site; entire streams (corridor + delta or swamp); all riparian corridors; and all deltas or swamps. Richness values are reported as mean per flat with error bars representing standard errors. Letters denote significant differences in mean species richness data for corridor and delta or swamp sites (lower case letters), entire streams (capitals), and all corridors and all delta or swamp sites (italicized capitals).

mean species richness than the undisturbed Meyers Branch corridor and the Savannah River swamp (Figure 2).

All corridor areas combined had greater seed bank mean species richness than all delta areas combined ($F_{1,67} = 67.16$, $P = 0.0001$). Seed banks of the planted and unplanted Pen Branch corridor sites did not differ in species richness, nor did they differ in richness from the seed bank of the Steel Creek corridor (Figure 2). In the delta areas, however, the seed bank richness in the planted sites was greater than in the unplanted sites and also greater (although not statistically significant) than in the Steel Creek delta sites.

Seed Bank Abundance

A total of 49,224 germinants, including 30 tree and shrub seedlings, emerged from the seed banks. The number of germinants differed among the sites ($F_{7,67} = 19.76$, $P = 0.0001$; Figure 3) and ranged from 748 individuals per m^2 in the undisturbed Savannah River swamp to 10,322 individuals per m^2 in the planted Pen Branch delta (Appendix 1). One species, *Lindernia dubia*, reproduced quickly and reseeded into the flats before individuals could be counted and removed, resulting in elevated densities of this species. Therefore, we removed it from the

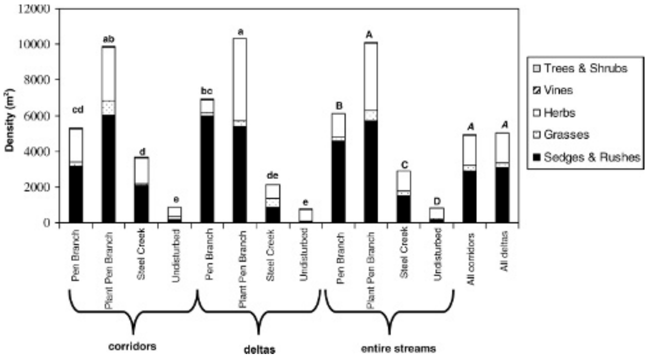

Figure 3. Density (mean number of individuals per m^2) of trees and shrubs, vines, herbs, grasses, and sedges and rushes germinating from the seed bank of the Pen Branch, Steel Creek, and the undisturbed Meyers Branch riparian corridor sites; Pen Branch and Steel Creek delta sites; the undisturbed Savannah River swamp site; entire streams (corridor + delta or swamp); all riparian corridors; and all deltas/swamps. Letters denote significant differences in mean density data for corridor and delta or swamp sites (lowercase letters), entire streams (capitals), and all corridors and all deltas (italicized capitals).

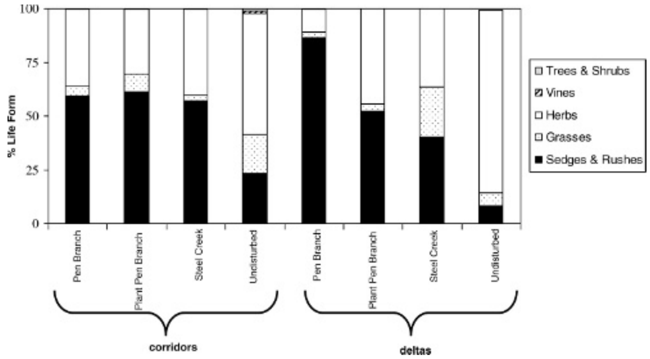

Figure 4. Percent of trees and shrubs, vines, herbs, grasses, and sedges and rushes germinating from the seed banks of the Pen Branch, Steel Creek, and the undisturbed Meyers Branch riparian corridor sites; Pen Branch and Steel Creek delta sites; and the undisturbed Savannah River swamp site. The percentage was calculated by dividing the number of plants of each life form by the total number of plants from the site.

seed bank abundance and community dissimilarity analyses.

When corridor and delta sites were grouped by stream, the mean number of individuals germinating was highest in Pen Branch, intermediate in Steel Creek, and lowest in Meyers Branch and the Savannah River swamp (Figure 3). Within Pen Branch, the mean number of individuals germinating from planted sites in the corridor and delta was greater than from the unplanted corridor and delta sites ($F_{1,34}$ = 17.14, P = 0.0001; Figure 3). All corridor areas combined did not differ in seed bank abundance from all delta areas combined (Figure 3).

Of the total individuals germinating from the seed banks, 57% were sedges and rushes, 36% were herbs, 6% were grasses, 0.3% were vines, and 0.06% were trees and shrubs. Sedges and rushes were the predominant life forms in the Pen Branch corridor unplanted (60%) and planted (61%) sites, in Pen Branch delta unplanted (86%) and planted (52%) sites, and in the Steel Creek corridor (57%) and delta (40%; Figure 4). Seed banks of the planted areas of Pen Branch (corridor and delta areas combined) produced eight woody germinants, and unplanted areas produced only one woody seedling.

The undisturbed Meyers Branch corridor and the Savannah River swamp had a greater proportion of herbs (56% and 85% in the corridor and swamp, respectively) in their seed banks (Figure 4). Also, the greatest number of woody seedlings germinated from these sites (11 from the corridor and nine from the swamp). *Taxodium distichum* germinated solely from the seed banks of Meyers Branch corridor and the Savannah River swamp.

Seed Bank Dissimilarities

Bray Curtis dissimilarities in the seed bank between sites differed for all but one comparison (Figure 5). In the delta area of Pen Branch, seed banks of planted and unplanted areas were similar (KW = 2.36, P = 0.16); however, when the importance of dominants was down-weighted by using the square root of Bray Curtis and Jaccard analyses, the dissimilarity between planted and unplanted delta sites became apparent (KW = 16.56, P = 0.0019). Seed banks from corridor and delta areas of disturbed streams (Pen Branch and Steel Creek) were more similar in composition than were the seed banks of either disturbed stream to the undisturbed Meyers Branch corridor and the Savannah River swamp (Figure 5). In both riparian corridor and delta areas, the unplanted Pen Branch sites were more similar to the mid-successional and the undisturbed sites than the planted Pen Branch sites were, but these differences were small.

When corridor and delta sites were grouped by stream, Pen Branch differed from Steel Creek, the undisturbed Meyers Branch corridor, and the Savannah River swamp (KW = 64.2, P = 0.01, and KW = 212.0, P = 0.0001, respectively). Similarly, Steel Creek, corridor and delta combined, differed from the undisturbed system (KW = 160.6, P = 0.0001). Finally, differences were observed when comparing all corridors to all deltas combined (KW = 61.6, P = 0.0001).

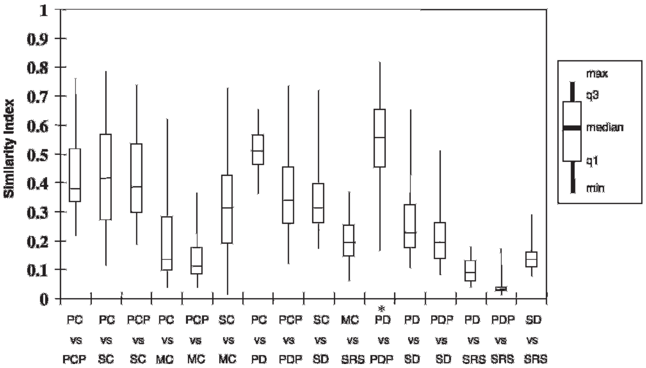

Figure 5. Similarity of seed bank composition between sites based upon Bray Curtis analysis. Similarity values are calculated by 1 – dissimilarity index. Box plots show median values, 25th (q1) and 75th (q3) quartiles, and minimum and maximum values (see legend). * = Not significant, $p > 0.05$. 1 = total similarity and 0 = total dissimilarity. Sites include the early successional unplanted Pen Branch corridor (PC), the planted Pen Branch corridor (PCP), the unplanted Pen Branch delta (PD), the planted Pen Branch delta (PDP), the mid-successional Steel Creek corridor (SC), the Steel Creek delta (SD), the undisturbed Meyers Branch corridor (MC), and the Savannah River swamp (SRS).

The vast majority of species present in seed banks of the undisturbed systems were represented in the seed banks of the more recently disturbed systems (Appendix 1). Only three species (*Mitchella repens*, *Taxodium distichum*, and *Nyssa aquatica*) were found in Meyers Branch and the Savannah River swamp, but not also observed in Pen Branch seed banks. In contrast, 16 species (11 herbs, four grasses, and one sedge) were observed in Pen Branch seed banks but were absent from the seed banks of the undisturbed areas.

DISCUSSION

Continued monitoring is integral to determine the long-term efficacy of restoration plans. In the short term, however, a chronosequence approach (substituting space for time) is suitable for an assessment of restoration success. Analysis of the soil seed bank as a measure of recovery is appropriate, as theoretical seed bank successional patterns have been well documented and provide a framework in which to evaluate the effectiveness of restoration.

We found that the abundance of seeds in the seed bank decreased along the successional gradient when corridor and delta sites were combined. Similarly, there was a decrease in species richness, although the mid-successional system did not have fewer species than the more recently disturbed system. This is consistent with successional theory and supports our first hypothesis that seed bank abundance and species richness would be greatest in Pen Branch, intermediate in Steel Creek, and lowest in Meyers Branch and the Savannah River swamp. Abernethy and Willby (1999) found a similar trend in river floodplain systems of northern Europe, where more intensely disturbed sites supported numerically large, species-rich seed banks, while less disturbed sites had smaller, species-poor propagule banks. Likewise, in a review of herbaceous and forested seed bank studies, Thompson (1978) reported a greater density of buried seeds in early successional systems and suggested that in frequently disturbed areas, species invest a high proportion of their resources in propagule production. In contrast, in more mature systems, shade becomes a limiting factor for many herbs and shrubs, and a decline in the density of buried seeds is to be expected (Thompson 1978).

The seed banks of all sites were dominated by herbaceous species (sedges, rushes, herbs, and grasses), while woody species were rare. This partially supports our second hypothesis that riparian seed banks would be dominated by herbaceous species; however, seed bank abundance and richness of woody species did not increase over the successional gradient. We found a somewhat greater presence of woody species in the undisturbed stream floodplain and swamp sites than in our disturbed sites, but these differences were not significant. Even in the undisturbed forested sites, woody seed abundances were lower than those reported for other southeastern riverine forest seed banks (Table 2). In a nearby *Taxodium distichum-Nyssa aquatica* swamp forest on the Savannah River floodplain, Schneider and Sharitz (1986) found densities of woody species ranging from 61 m^{-2} to 201 m^{-2} in the seed bank. These included four tree and two shrub species, although herbaceous species were most abundant. Furthermore, Titus (1991) reported seed bank densities of woody species ranging from 127 m^{-2} to 611 m^{-2} in a hardwood floodplain swamp in Florida (Table 2). Our collection of samples in the late spring to mid-summer may have contributed to the low seed bank densities of certain woody riparian and swamp species (e.g., *Carya* spp., *Liriodendron tulipifera*, *Liquidambar styraciflua*, *Nyssa* spp., *Taxodium distichum*, and *Quercus* spp.), which characteristically disperse seeds later in the growing season (Schopmeyer 1974). However, soil collection dates should have been synchronous with seed dispersal windows for other species noticeably absent from the seed banks but abundant in the standing vegetation (e.g., *Acer rubrum*, *Betula nigra*, and *Salix nigra*).

Table 2. Density (m^{-2}), richness, and location of riparian and swamp seed banks from our study and those from the literature.

Wetland	Density	Richness	Site	Reference
Riparian/Swamp	4854	61	SC	This study
Riparian	11	1	AK	Walker et al. 1986
Riparian	*	58	PA	Hanlon et al. 1998
Riparian	1724	55	OR	Harmon and Franklin 1995
Swamp	100	6	GA	Gunther et al. 1984
Swamp	2576	59	SC	Schneider and Sharitz 1986
Swamp	127–611	10	FL	Titus 1991**
Swamp	270	18	MA	LaDeau and Ellison 1999
Swamp	*	173	IL	Middleton 2003

*= Not calculated.
**= Herbaceous germinants not counted.

Low seed bank densities of woody species have been reported in other forested wetlands, however, including *Taxodium distichum* swamps along the Cache River in Illinois (Middleton 2003) and northern riparian forests (Harmon and Franklin 1995, Hanlon et al. 1998). Thompson (1978), however, reported a consistent absence of tree species in studies of various North American forest seed banks and suggested that seeds of temperate deciduous trees are remarkably short-lived by comparison with the majority of herbaceous species. This trend may also be related to the increase in seed predation as mature forests develop (Milberg 1995).

Overall, the mean seed bank richness and density values we found are some of the highest reported for North American riparian and swamp seed bank studies (Table 2). Seed banks dominated by herbaceous species may reflect the large, persistent seed pools of early successional, annual, and biennial plants that rapidly establish following disturbance events, and remain viable often long after aboveground populations disappear. The conspicuous shift from sedge- and rush-dominated seed banks of the more recently disturbed areas to the herb-dominated seed banks of the undisturbed areas appears to be attributable to an overall decline (though not a proportionally uniform decrease for all life forms) in seed bank abundance, rather than the influx of novel herb species into the seed banks of undisturbed areas. As such, the seed banks of the most recently disturbed areas show potential to reestablish mature herbaceous vegetation.

Within the most recently disturbed system (Pen Branch), the mean number of germinants was greater in planted than in unplanted sites, although seed bank species richness did not differ. Thus, our third hypothesis, that seed banks of planted sites within Pen Branch would have greater abundance of propagules and species richness than those of unplanted sites, was only partly supported. When the corridor and delta regions of Pen Branch were combined, planted sites had 41% more germinants than unplanted sites and were dominated by early successional sedges and rushes. Dense stands of early successional herbaceous species may arrest forest succession by depriving woody seedlings of light and space (Gunderson 1984, Dunn and Sharitz 1987). The dissimilarities between planted and unplanted sites cannot be attributed to seed input from the planted seedlings, as neither of the woody species emerging from the seed banks in the planted areas (*Rhus copallinum* and *Liriodendron tulipifera*) was planted as part of the restoration effort.

The high seed densities in the planted sites of the Pen Branch riparian corridor may be attributable in part to site preparation treatments. Prior to the 1993 plantings, burning and herbicide treatments were conducted to remove the standing vegetation and reduce competitive stresses on the newly planted seedlings. These treatments may have set back the successional development of the planted areas relative to their unplanted counterparts, by inciting germination cues favoring early successional, ruderal species. In addition, the absence of aboveground competition following the treatments may have allowed early colonizing species to thrive and establish large soil seed reserves.

High seed bank densities in planted areas of the Pen Branch delta were due primarily to the great abundance of *Typha latifolia* germinants. Previous studies have shown that *Typha* may have persistent seed banks (van der Valk and Davis 1979) and an extensive rhizome system. Similar to these findings, delta site preparation treatments (herbicide) that removed the standing vegetation may have provided ideal conditions for *Typha* germination or rhizome growth and thus promoted the presence of this species in the seed bank.

Riparian corridor sites had greater seed bank species richness than the delta areas, although seed bank abundances were not different within a particular system. It is likely that the delta and swamp areas experience more prolonged inundation than do the corridor sites, as they are subject to recurring flooding from the Savannah River (Sharitz et al. 1974b). In wetlands, seed banks may exhibit higher density and diversity in areas of variable hydrologic conditions (van der Valk and Davis 1978, Pederson 1981, La Peyre et al. 2005) and substrate heterogeneity, such as those found in the riparian corridor (Schneider and Sharitz 1986, Leck and Simpson 1987, Kirkman and Sharitz 1994, Harmon and Franklin 1995, Vivian-Smith 1997), than under more stable conditions such as those found in deltas and swamps (van der Valk and Davis 1979, Leck 1989, Collins and Wein 1995, Casanova and Brock 2000, Capon and Brock 2006).

Decreases in seed abundance and species richness were found across the wetland successional gradient, thereby conforming to successional trends. The seed banks were dominated by herbaceous species in all sites, and woody species were rare, even in mature wetland forest areas. Though dominated by sedges and rushes, Pen Branch planted areas had greater seed bank abundances than unplanted areas. The dominance by early successional species at planted sites may be an unintended consequence of site preparation treatments. This should not be interpreted as a reason not to undertake such restoration efforts in disturbed wetland sites, but consequences of site preparation should be recognized and weighed during the development of restoration plans. Future research should assess the seed bank and extant vegetation to determine if planting has hastened the recovery over the long term.

ACKNOWLEDGMENTS

This research was supported by the U.S. Department of Energy (WSRC/ERDA subcontract C001571-O) and Financial Assistance Award Number DE-FC09-96SR18546 between the U.S. Department of Energy and the University of Georgia. We thank Eric Nelson for assistance with funding, Philip Dixon for advice on sampling protocol, Juanita Blocker for assistance with graphics, and Tom Philippi and Beverly Collins for statistical advice. We especially thank Patrick Sweeney of the University of Georgia herbarium for assistance in identifying plant specimens and Paul Stankus, who provided critical support in seed bank sampling and identification of seedlings. We appreciate the field assistance given by Bruce Allen, Dan Coughlin, Virginia Jin, Frederick Jones, Harold Jones, Nathan MacArthur, Denise Palleiko, Melissa Quillen, Julian Singer, and Laura Uhrich. Finally, we thank Brian Palik and an anonymous reviewer for many useful comments that improved the manuscript.

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Manuscript received 23 March 2006; revision received 6 September 2006; accepted 31 October 2006.

Appendix 1. Total number of plants germinated from corridor and delta riparian seed banks from sites along a successional gradient. Sampling locations range from a recently disturbed system that has been allowed to naturally revegetate (Pen Branch) and has been partially "restored" (Planted Pen Branch = Pen Plant), to a system undergoing natural recovery from similar disturbance for more than 30 years (Steel Creek), to undisturbed systems (Meyers Branch and the Savannah River swamp). Values are the total number of germinants from 10 macro-samples per site (see text for explanation of sampling design).

	Corridor				Delta			
Growth-Form and Species	Pen Branch	Pen Plant	Steel Creek	Meyers Branch	Pen Branch	Pen Plant	Steel Creek	Savannah River
Herbs								
Ammannia coccinea Rottb.	648	463	103	6	2	7	5	0
Azolla caroliniana Willd.	76	10	23	8	0	4	1	40
Bidens tripartita L.	1	2	7	0	0	0	0	7
Boehmeria cylindrica (L.) Sw.	150	216	19	48	0	1	9	11
Brassicaceae (unknown 1)	37	92	10	5	0	3	0	0
Cardamine hirsuta L.	2	0	0	2	0	2	0	3
Eclipta prostrata (L.) L.	1	0	1	3	1	0	0	0
Elodea canadensis Michx.	54	0	0	0	0	0	0	0
Erechtites hieraciifolia (L.) Raf. ex DC	4	11	0	1	0	0	0	3
Eupatorium capillifolium (Lam.) Small	99	127	51	4	0	17	2	0
Gamochaeta falcata (Lam.) Cabrera	7	13	19	12	0	1	10	4
Geranium carolinianum L.	9	0	0	1	0	0	0	0
Hydrocotyle umbellata L.	4	1	11	0	16	13	0	5
Hypericum mutilum L.	435	1309	544	124	18	215	22	12
Lemna perpusilla Torr.	0	0	0	0	47	0	0	433
Lindernia dubia (L.) Pennell*	15864	1953	11341	1960	52	299	277	287
Ludwigia alternifolia L.	105	250	85	4	0	18	20	0
Ludwigia decurrens Walt.	295	535	200	18	90	183	84	0
Ludwigia glandulosa Walt.	71	143	103	61	18	35	11	15
Ludwigia leptocarpa (Nutt.) Hara	8	4	1	0	0	60	22	0
Ludwigia palustris (L.) Ell.	344	356	311	89	17	38	31	143
Ludwigia spp.	11	12	24	4	35	75	125	0
Ludwigia spathulata Torr. & Gray	9	19	1	0	0	3	0	0
Micranthemum umbrosum (J.F. Gmel.) Blake	27	12	103	59	0	3	0	0
Mitchella repens L.	0	0	0	5	0	0	0	0
Mitreola petiolata (J.F. Gmel.) Torr & Gray	6	27	0	8	0	1	0	0
Mollugo verticillata L.	16	66	15	15	0	1	0	0
Murdannia keisak (Hassk.) Hand.-Maz.	25	89	23	0	11	40	198	4
Myriophyllum aquaticum (Vell.) Verdc.	0	0	0	0	0	0	0	2
Oldenlandia uniflora L.	5	0	17	0	0	8	0	0
Peltandra virginica (L.) Schott	0	0	0	3	3	0	0	4
Pluchea camphorata (L.) DC.	6	8	4	17	0	0	0	0
Polygonum hydropiper L.	42	145	29	6	58	96	147	3
Polygonum punctatum Ell.	14	0	3	0	0	0	0	0
Polypremum procumbens L.	20	62	195	31	5	2	9	0
Ptilimnium capillaceum (Michx.) Raf.	0	0	1	0	0	1	0	0
Rotala ramosior (L.) Koehne	0	5	19	0	0	34	30	0
Sagittaria spp.	4	2	14	75	74	667	248	154
Samolus valerandi L.	14	13	0	10	0	0	0	0
Senna obtusifolia (L.) Irwin & Barneby	0	0	0	0	0	1	0	0
Solidago spp.	0	4	0	7	0	0	0	2
Sphenoclea zeylandica Gaertn.	5	0	0	0	3	5	0	0
Typha latifolia L.	2	8	5	8	84	4623	53	8
Viola spp.	1	0	0	0	0	0	0	0

Appendix 1. Continued.

Growth-Form and Species	Corridor				Delta			
	Pen Branch	Pen Plant	Steel Creek	Meyers Branch	Pen Branch	Pen Plant	Steel Creek	Savannah River
Unknown herb	21	17	26	24	18	31	30	4
Herb germinants (total)	**2578**	**4021**	**1967**	**658**	**500**	**6188**	**1057**	**857**
Herb density m^2	**1906.8**	**2974.1**	**1455.0**	**486.7**	**740.0**	**4577.0**	**782.0**	**633.9**
Herb species richness	**37**	**31**	**31**	**30**	**18**	**31**	**20**	**20**
Grasses								
Andropogon spp.	73	0	4	0	0	0	0	0
Dichanthelium boscii (Poir.) Gould & C.A. Clark	0	1	0	0	0	0	0	0
*Dichantheliu*m spp.	0	0	0	0	0	3	0	0
Panicum spp.	84	207	23	21	58	408	85	59
Paspalum fluitans (Ell) Kunth	0	0	0	0	10	0	0	0
Poaceae (unknown 1)	161	906	105	189	61	42	588	2
Grass germinants (total)	**318**	**1114**	**132**	**210**	**129**	**453**	**673**	**61**
Grass density m^2	**235.2**	**824.0**	**97.6**	**155.3**	**191.0**	**335.1**	**498.0**	**45.1**
Grass species richness	**3**	**3**	**3**	**2**	**3**	**3**	**2**	**2**
Sedges and Rushes								
Cyperaceae (unknown 1)	1997	3729	1129	134	2906	5991	951	82
Cyperus polystachyos Rottb. var. texensis (Torr.) Fern.	7	0	69	10	1	0	0	0
Juncaceae (unknown 1)	2308	4429	1626	128	1126	1295	215	2
Scirpus cyperinus (L.) Kunth	0	0	0	0	0	3	0	0
Sedge/Rush germinants (total)	**4312**	**8158**	**2824**	**272**	**4033**	**7289**	**1166**	**84**
Sedge/Rush density m^2	**3189.3**	**6034.0**	**2089.0**	**201.2**	**5966.0**	**5391.0**	**862.0**	**62.1**
Sedge/Rush species richness	**3**	**2**	**3**	**3**	**3**	**3**	**2**	**2**
Trees and Shrubs								
Liriodendron tulipifera L.	0	0	0	4	0	4	0	0
Nyssa aquatica L.	0	0	0	0	0	0	0	2
Rhus copallinum L.	0	3	0	2	0	1	0	0
Taxodium distichum (L.) L.C. Rich.	0	0	0	3	0	0	0	6
Woody (unknown 1)	0	0	1	2	1	0	0	1
Tree/Shrub germinants (total)	**0**	**3**	**1**	**11**	**1**	**5**	**0**	**9**
Tree/Shrub density m^2	**0**	**2.21893**	**0.74**	**8.1361**	**1.48**	**3.698**	**0**	**6.6568**
Tree/Shrub species richness	**0**	**1**	**1**	**4**	**1**	**2**	**0**	**3**
Vines								
Mikania scandens (L.) Willd.	30	41	23	15	8	21	2	0
Vine germinants (total)	**30**	**41**	**23**	**15**	**8**	**21**	**2**	**0**
Vine density m^2	**22.2**	**30.3**	**17.0**	**11.1**	**11.8**	**15.5**	**1.5**	**0.0**
Vine species richness	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**0**
All Species								
Total germinants**	**7238**	**13337**	**4947**	**1166**	**4671**	**13956**	**2898**	**1011**
Total density m^2	**5353.6**	**9864.6**	**3659.0**	**862.4**	**6910.0**	**10322**	**2143**	**747.8**
Total species richness**	**44**	**38**	**39**	**40**	**26**	**40**	**25**	**27**
Total germinants	**49224**							
Total average density m^2	**4854.4**							

**Lindernia dubia* reproduced quickly and reseeded into the flats before individuals could be counted and removed, resulting in elevated densities of this species. Therefore, we removed *Lindernia dubia* from the seed bank abundance analysis.
**Totals for all species are calculated from the 10 macro-samples for all sites (80 samples).